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Moniliophthora aurantiaca sp. nov., a Polynesian species occurring in littoral forests

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Abstract — A new species of *Moniliophthora* is described from the Samoan Islands. The new species is characterized by its bright orange pileus and pale orange stipe and lamellae. It occurs commonly on woody debris in moist littoral forests and has not been found in upland forests. A phylogenetic analysis of nLSU and ITS sequences indicates that *Moniliophthora aurantiaca* has an affinity with the Central and South American members of the genus. Possible mechanisms for the dispersal of fungi from the Neotropics to the Samoan Islands are discussed.

Key words — *Agaricales*, American Samoa, *Crinipellis*, Oceania, phylogeny

Introduction

The mycobiota of the Samoan Islands has received very little attention. What work that has been done consists of an inventory of the wood decay fungi and plant pathogens present in American Samoa (Brooks 2004, 2006) along with the recent description of an *Inocybe* species from the island of Ta'u (Kropp & Albee-Scott 2010). Our preliminary work on Samoan fungi indicates that the mycoflora of the islands is potentially quite rich and that a number of undescribed species is present.

An attractive, bright orange species of *Moniliophthora* was recently discovered in littoral forest on the islands of Tutuila and Ta'u, American Samoa. In spite of its distinctive appearance and the fact that it appeared to be very common at the time the material was collected, no name has been found for this fungus among the published species of the *Moniliophthora*/*Crinipellis* complex. In this article, we propose a new species of *Moniliophthora* from the Samoan Islands and assess its phylogenetic position relative to other members of *Moniliophthora* and to members of *Crinipellis* and *Chaetocalathus*.

Materials & methods

Specimens were photographed in the field on natural substrates or using a gray card as a background and field notes were taken while the material was still fresh. The collections were then dried for herbarium specimens. Microscopic study of the dried specimens was carried out in the laboratory using a light microscope after rehydrating tissue sections in Melzer's reagent. Microscopic characters were measured using oil immersion at 1000× except for pileus hairs, which because of their length were made at lower magnifications. All microscopical characters were illustrated with the aid of a drawing tube. Spore measurements are given as an average with ranges, whereas measurements of the other cells are given as ranges. Color notations were taken from the digital photographs using the Munsell Soil Color Charts (Munsell Color 2000) and Farver i Farver (Wanscher & Kornerup 1991). Formats for the Munsell and Farver i Farver color notations are 5YR 8/8 and 54A respectively. All specimens examined, including the holotype, have been accessioned into the Intermountain Herbarium (UTC) at Utah State University.

DNA was extracted from dried herbarium material using standard protocols adapted for use in our lab (Kropp et al. 1996). Amplified PCR products were obtained using standard PCR protocols (White et al. 1990) for the internal transcribed spacer (ITS) using primers ITS4 and ITS5 (White et al. 1990) and for the nuclear large ribosomal subunit (nLSU) between primers LROR and LR5 (Moncalvo et al. 2000). Direct sequencing of the purified PCR products was done for both the nLSU and the ITS using the amplification primers. Both sequences for *M. aurantiaca* were deposited in GenBank (ITS = JN692482, nLSU = JN692483).

Twenty-one species of *Crinipellis* representing Europe, Australasia, and North and South America were sampled. Taxon sampling also included four *Moniliophthora* species from Australasia, North America, and the American tropics. To identify apomorphies, members of the closely related *Chaetocalathus* and representatives of the less closely related *Tetrapyrgos* and *Marasmius* were used as outgroups in our analysis (Table I).

Clustal X (Thompson et al. 1997) was used to align the nLSU and ITS sequences after they were concatenated in the phylogenetically uninformative terminal ends. MrBayes 3.1 was used to analyze the aligned data set, 1613 bases in length (Ronquist & Huelsenbeck 2003). Treespace was searched using a time reversible model of evolution (Maddison 1994, Rodriguez et al. 1990) and a discrete gamma distribution with six substitution types and some invariant sites (GTR+G+I). Every hundred trees were sampled from the Bayesian simulation to approximate posterior probabilities. The trees were simulated using the Markov Chain Monte Carlo Method (MCMC) and all Bayesian simulations were conducted with eight active MCMC chains, heated at 0.2, and started with a randomly chosen neighbor-joining tree. The first MCMC run was iterated for 1,000,000 generations and three subsequent MCMC simulations were done using 1,000,000 generations, sampling every one hundredth tree. A majority consensus tree was calculated from the last 7000 sampled trees from a 10,000 tree data set using all runs to recover the posterior probabilities of the internal nodes using the SUMT command in MrBayes. All four consensus trees recovered from the four Bayesian simulations were phylogenetically identical. The resulting statistics showed that the two independent MCMC chains converged with a standard deviation <0.001 (Ronquist & Huelsenbeck

Table 1. Species, geographic origins, and GenBank accession numbers

Taxon	Origin	ITS	nLSU
Chaetocalathus columellifer (Berk.) Singer	Malaysia	FJ167665	FJ167665
Ch. cf. *columellifer*	Ecuador	AY916686	—
Ch. craterellus (Durieu & Lév.) Singer	Italy	FJ167664	—
Ch. fragilis (Pat.) Singer	Thailand	FJ167662	—
Ch. galeatus (Berk. & M.A. Curtis) Singer	Thailand	FJ167663	—
Ch. liliputianus (Mont.) Singer	Puerto Rico	AY916682	AY916680
Ch. magnus Halling	Colombia	FJ167666	—
Crinipellis actinophora (Berk. & Broome) Singer	Malaysia	FJ167626	—
Cr. brasiliensis Arruda et al.	Brazil	AY317137	—
Cr. brunneipurpurea Corner	Indonesia	FJ167646	—
Cr. brunnescens Kerekes & Desjardin	Indonesia	FJ167627	—
Cr. campanella (Peck) Singer	—	—	AF042647
Cr. cupreostipes Kerekes et al.	Thailand	FJ167641	—
Cr. dipterocarpi Singer	Thailand	FJ167651	—
Cr. furcata Kerekes et al.	Indonesia	FJ167658	—
Cr. cf. *iopus* Singer	Papua NG	FJ167639	—
Cr. malesiana Kerekes et al.	Malaysia	FJ167629	—
Cr. maxima A.H. Sm. & M.B. Walters	—	—	AF042630
Cr. piceae Singer	N. America	FJ167633	—
Cr. procera G. Stev.	New Zealand	FJ167660	—
Cr. scabella (Alb. & Schwein.) Murrill	Europe	FJ167635	AM946420*
Cr. setipes (Peck) Singer	Thailand/USA	FJ167634	AY916689**
Cr. stipitaria (Fr.) Pat.	Germany	AY571033	AY207194
Crinipellis sp.	Thailand	AY916698	—
Crinipellis sp.	Guyana	AY916701	—
Cr. tabtim Kerekes et al.	Thailand	FJ167643	—
Cr. trichialis (Lév.) Pat.	Indonesia	FJ167609	—
Cr. zonata (Peck) Sacc.	Canada	AY916692	AY916690
Marasmius apatelius Singer	Thailand	EU935561	—
M. leucorotalis Singer	Malaysia	FJ431253	—
M. rotula (Scop.) Fr.	N. America	DQ182506	DQ457686
Moniliophthora aurantiaca	Samoa	JN692482	JN692483
M. canescens (Har. Takah.) Kerekes & Desjardin	Malaysia	FJ167668	—
M. perniciosa (Stahel) Aime & Phillips-Mora	Peru	AF335590	—
M. roreri (Cif.) H. C. Evans et al.	Costa Rica	AY916746	AY916744
Moniliophthora sp.	N. America	AY916754	—
Tetrapyrgos nigripes (Fr.) Horak	N. America	DQ449942	AF261337
T. subcinerea (Berk. & Broome) Horak	S. E. Asia	EF175552	—
T. subdendrophora (Redhead) Horak	N. America	EF175521	—

* ITS sequence from a German collection, nLSU from an Estonian collection
**ITS sequence originated from a Thai collection, nLSU sequence from a North American collection.

2003). The potential scale reduction factors for all convergence statistics approached 1.001 for all parameters. Posterior probability support measures <50% are not shown. *Tetrapyrgos* was used to root the consensus tree.

Results

The results of the Bayesian analysis show that the undescribed species clusters with the *Moniliophthora* clade, which has very good posterior probability support (Fig. 1). Certain other taxa, such as *Crinipellis* aff. *iopus* and *Crinipellis brasiliensis* (which have not yet been transferred to *Moniliophthora*), also clustered within this clade. Our analysis indicates that *M. aurantiaca* has a stronger affinity with the neotropical members of the clade such as *M. roreri* than it does with the Australasian representatives such as *M. canescens* or *Crinipellis* aff. *iopus*. *Moniliophthora aurantiaca* is closely related to *M. roreri,* which has a neotropical distribution. In addition, two other neotropical taxa, *M. perniciosa* and *Crinipellis brasiliensis,* appear to be close relatives of *M. aurantiaca* based on our analyses.

The species of *Chaetocalathus* and *Marasmius* formed two well-supported clades basal to *Crinipellis* and *Moniliophthora*. In our analysis, the members of *Moniliophthora* occupy a clade derived from within *Crinipellis*. Based on these results, accepting *Moniliophthora* as a genus renders *Crinipellis* paraphyletic, although the node separating *Crinipellis* clade 1 from *Crinipellis* clade 2 and *Moniliophthora* is not well supported (Fig. 1).

Discussion

Moniliophthora aurantiaca is an unusually conspicuous element of the mycobiota of American Samoa. It stands out primarily because of its bright orange colors but also because it fruits commonly in littoral forests. Thus far, it has been found only in a narrow strip of damp littoral forest situated along the shoreline on the islands of Tutuila and Ta'u, American Samoa. In one instance, it was found among trees growing on a rocky outcrop a few meters above the water but still at the shoreline. That *M. aurantiaca* was never found outside the littoral zone in spite of an abundance of apparently suitable moist woody substrates in nearby higher elevation forests suggests a halophilic or maritime beach ecology. Known thus far only from American Samoa, *M. aurantiaca* may be endemic to the Samoan Islands, but its distribution is still poorly known and further work is needed to confirm whether it is really an endemic species.

The species belongs to the *Moniliophthora*/*Crinipellis* complex that currently comprises five *Moniliophthora* species and 163 *Crinipellis* species (http.//www.indexfungorum.org/). Of these, *M. aurantiaca* macroscopically most closely resembles the South American species *Crinipellis ticoi* Halling, which is also orange in color. Despite their macroscopic similarities, *C. ticoi* differs from *M. aurantiaca* microscopically in larger spores (12.1–14.3 × 5–7.1 μm) and

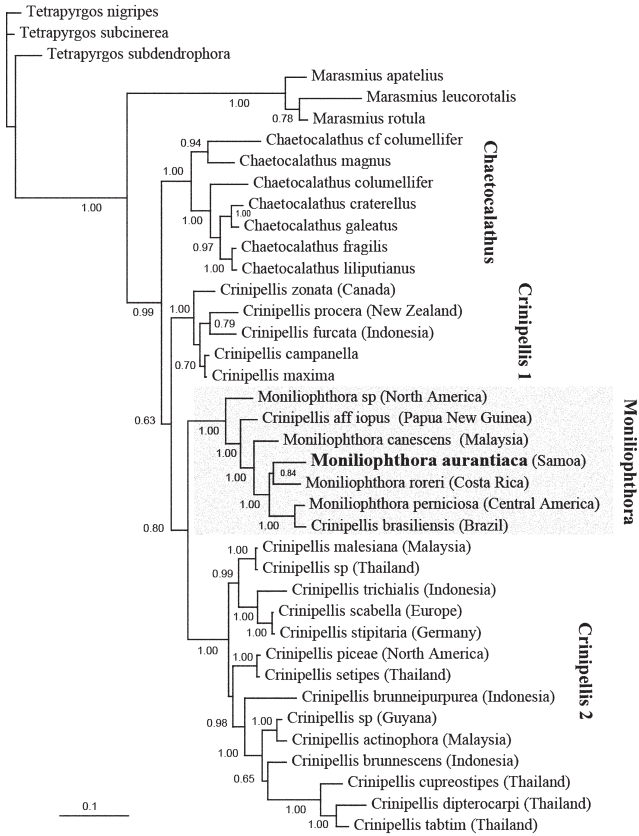

Figure 1. Phylogram from a Bayesian analysis of a combined ITS and nLSU dataset for *Crinipellis*, *Moniliophthora*, and *Chaetocalathus*. Support measures are shown for nodes with 60 percent or greater posterior probability support. Members of *Tetrapyrgos* were used to root the phylogram.

cheilocystidia that lack the apical appendages present on the cheilocystidia of *M. aurantiaca* (Fig. 3). One other orange *Crinipellis* is the African *C. hygrocyboides* (Henn.) Singer. Neither Hennings (1902) nor Singer (1989) gives microscopic details or a detailed description for this fungus, making comparisons with other taxa difficult. Since Halling (1993) reports that spores and cystidia were not observed in the type material of *C. hygrocyboides* from the Muséum National d'Histoire Naturelle, we have studied isotype material of *C. hygrocyboides* (≡*Marasmius hygrocyboides* Henn.) from the Royal Botanical Gardens, Kew. The specimen resembles *M. aurantiaca* but differs by having a mixture of long dextrinoid hairs and clavate, thin-walled dextrinoid cystidia on the stipe surface and similar, but slightly smaller, spores. We were unable to

reliably study cheilocystidia in the *C. hygrocyboides* material due to difficulty reviving the material. However, all cells at the lamellar edges appeared to be clavate and different from the cheilocystidia with apical appendages of *M. aurantiaca.* It would be very useful to have molecular data for this species to determine whether it belongs to the *Moniliophthora* clade. Another similar taxon is *M. canescens,* which has orange hues when wet but is typically brownish; additional differences include an initially white stipe that becomes brown and narrower spores (Takahashi 2000). *Crinipellis malesiana,* which also develops orange colors in age (Kerekes & Desjardin 2009), is phylogenetically separate from *M. aurantiaca* (Fig. 1).

Based on our phylogenetic analysis, *M. aurantiaca* falls within the *Moniliophthora* clade of Aime & Phillips-Mora (2005). These workers found that fungi belonging to *Moniliophthora*, which had been used for an anamorphic pathogen of cocoa (Evans et al. 1978), are not only closely allied to certain members of *Crinipellis* but form a distinct lineage with *Crinipellis* in the *Marasmiaceae* for which they proposed using *Moniliophthora* as a generic name. The genus currently includes both conidial and agaricoid taxa. The agaricoid members of *Moniliophthora* are usually relatively brightly colored species that would otherwise have been placed in section *Iopodinae* of *Crinipellis.*

In contrast, our analysis indicates that *Moniliophthora* does not occupy a distinct lineage but is derived from within *Crinipellis*. In this case, accepting *Moniliophthora* as a genus makes *Crinipellis* paraphyletic (Fig. 1). Based on our results, one could abandon *Moniliophthora* and transfer everything in it, including the anamorphic species, to *Crinipellis*. However, one cannot ignore that the ITS analysis of Kerekes & Desjardin (2009) and the 5-gene phylogeny of Aime & Phillips-Mora (2005) both agree that the *Moniliophthora* clade forms a distinct lineage. In addition, the node separating the two *Crinipellis* clades shown in our phylogram has weak posterior probability support (Fig. 1). Given the discrepancy between our analysis and the other two studies, further work is needed to clarify relationships in the *Moniliophthora/Crinipellis* complex. For now, the preponderant information indicates that the *Moniliophthora* clade forms a distinct lineage and until further work is done we retain *Moniliophthora* as a genus in the sense of Aime & Phillips-Mora (2005).

Caution must be used when using our phylogram to identify biogeographical patterns. Nonetheless, the close affinity of *M. aurantiaca* to the pathogenic South and Central American members of the *Moniliophthora* clade is well supported and implies that either *M. aurantiaca* or an ancestral taxon originated in the neotropics (Fig. 1). This is somewhat unexpected, because we earlier found that another Samoan fungus, *Inocybe tauensis* Kropp & Albee-Scott (2010), has paleotropical roots and because Samoan plant communities have Australasian ties (Van Balgooy et al. 1996).

Regardless of where *M. aurantiaca* originated, long-distance dispersal was clearly involved because the islands are relatively young and have never been connected to a land mass (McDougall 1985). In recent times, humans could have carried *M. aurantiaca* to the Samoan Islands on plants or in woody materials from almost any part of the world. However, long-distance dispersal might also have occurred via other well-known mechanisms. Rafting is one potential means of transport because *M. aurantiaca* grows in woody debris and could be carried long distances by floating wood. Rafting is known to transport organisms and is thought to have resulted in the dispersal and subsequent cladogenesis of snails across large areas of the Pacific Ocean, including an endemic Samoan snail (Donald et al. 2005). In another instance, an oyster species is thought to have been carried via rafting from Chile to New Zealand (Foighil et al. 1999). Thus, a plausible mechanism exists for the dispersal of fungi from the Neotropics to Samoa. The mycelium of *M. aurantiaca* could have been carried within woody material from South America to Samoa via the South Equatorial Current that has a general westward flow across tropical portions of the South Pacific. Airborne spores are another means by which agarics could potentially cross the Pacific and it is clear that fungal spores can travel long distances with air masses (Brown & Hovmøller 2002). If *M. aurantiaca* has neotropical roots, then its spores or those of an ancestral taxon would have needed to cross the Pacific from the east to get to the Samoan Islands. The easterly trade winds of the equatorial South Pacific provide another plausible mechanism by which this could have happened.

Taxonomy

Moniliophthora aurantiaca Kropp & Albee-Scott, **sp. nov.** Figs 2, 3

Mycobank MB563345

Differs from *Crinipellis ticoi* by its smaller basidiospores and cheilocystidia with apical appendages and from *Crinipellis hygrocyboides* by its short, moderately thick-walled setae-like stipe hairs and the absence of clavate caulocystidia.

Type: American Samoa, National Park of American Samoa, Ta'u Unit, in littoral forest along trail to Si'u point, on woody debris, 17 May 2009, leg. B.R. Kropp BK17-May-2009-20a (**Holotype** UTC253631; GenBank JN692482, JN692483).

Etymology: *aurantiaca* refers to the bright orange coloration of the pileus.

Pileus 3–15 mm diameter, convex with margin somewhat inrolled at first then broadly convex to nearly plane, disc with a small umbo, sometimes slightly depressed around the umbo, translucent-striate or slightly sulcate from the margin nearly to the disk, surface matted fibrillose; bright red orange (78A, 2.5YR 7/12) at the center, becoming pale orange (54A, 5YR 8/8) toward the margin especially in age; when dry, pale orange with the umbo darker. Lamellae narrowly attached, subdistant, pale orange (65A, 5YR 8/8), very

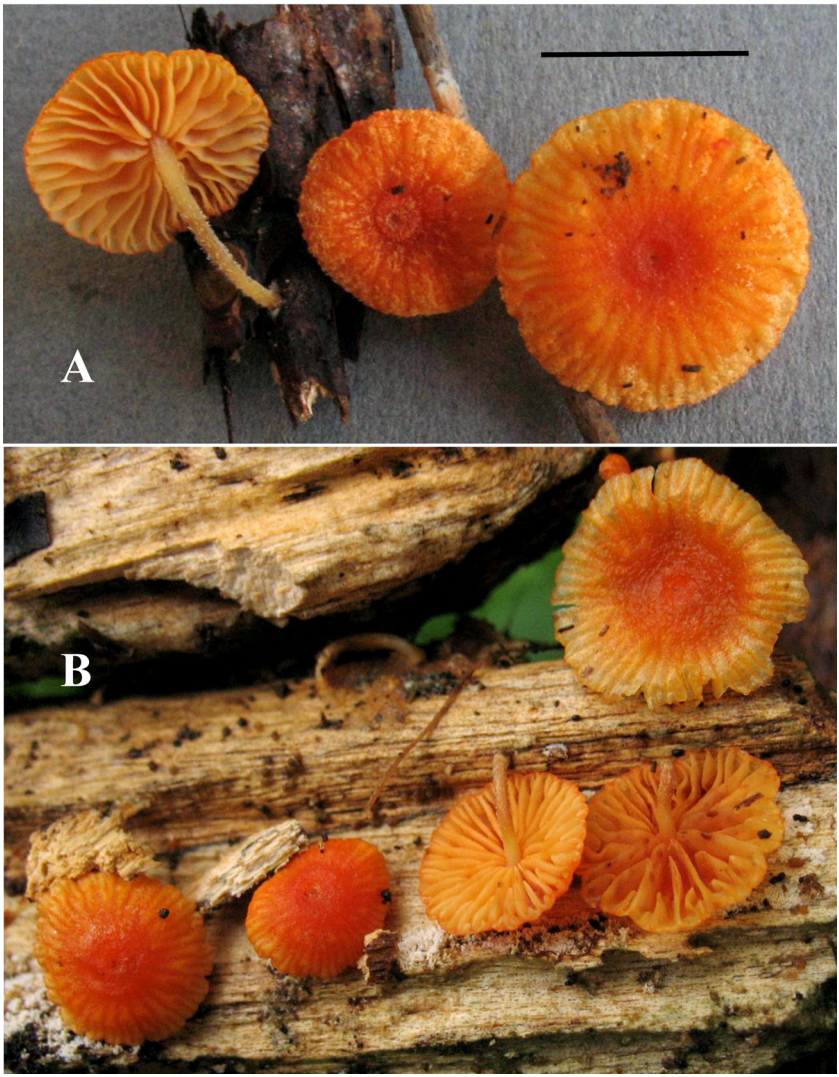

Figure 2. *Moniliophthora aurantiaca*. Basidiomata: A. UTC253824; B. UTC253809. Scale = 1 cm.

pale orange when dry; lamellulae in 1–2 series. Stipe 5–8 × 0.25–1 mm, central, terete, equal, densely pruinose, concolorous with the lamellae except for the base which is often brown, extreme base on some specimens strigose, stipe inserted for most specimens. Pileipellis a cutis of fairly loosely woven light brown, lightly encrusted hyphae 5–8 µm wide, not well differentiated

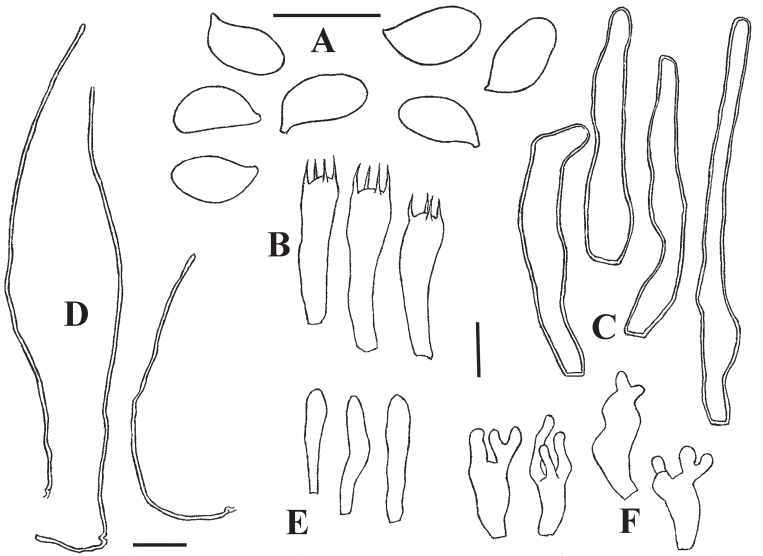

Figure 3. *Moniliophthora aurantiaca*. A. Basidiospores B. Basidia C. Stipe hairs D. Pileipellis hairs E. Basidioles F. Cheilocystidia. Scales: D = 50 μm; A–C, E, F = 10 μm.

from the pileus context; numerous long, dextrinoid hairs present, these with a basal clamp and 400–600 × 4–5 μm, mostly hyaline not greenish in KOH; context not dextrinoid. Lamellar trama subparallel to interwoven; hyphae hyaline sometimes lightly encrusted, clamped, 4–8 μm wide; context not dextrinoid. Stipe tissue parallel, smooth, hyaline, hyphae 4–8 μm wide; dextrinoid to weakly dextrinoid; stipe hairs numerous, covering the stipe apex and base, dextrinoid to weakly dextrinoid, short and moderately thick-walled, resembling setae, 52–85 × 5–10 μm. Basidiospores 7.5–(8.7)–11.0 × 4–(4.6)–6.0 μm, Q = 1.8–2.1, amygdaliform, thin-walled, smooth, hyaline, inamyloid. Basidia 26–30 × 6–7 μm, clavate, typically four-spored. Basidioles 22–25 × 4–5 μm, clavate. Pleurocystidia none. Cheilocystidia 20–22 × 5–8 μm, numerous, hyaline, thin-walled, typically with several irregular apical, finger-like appendages. Clamps present. Rhizomorphs absent.

Habitat and distribution occurring on fallen twigs and other woody material in littoral forest.

Additional specimens examined—**AMERICAN SAMOA**. **Tutuila**, near Vaitogi, on woody debris in wooded area near shoreline, 11 May 2009, leg. B.R. Kropp, BK11-May-2009-11 (UTC253809); National Park of American Samoa, Tutuila Unit, on woody debris in littoral forest along trail to Pola Island, 12 May 2009, leg. B.R. Kropp, BK12-

May-2009-12 (UTC253824); BK12-May-2009-16 (UTC253828); BK12-May-2009-18 (UTC253830); BK12-May-2009-17 (UTC253829). **Ta'u**, National Park of American Samoa, Ta'u Unit, on woody debris in littoral forest along trail to Si'u point, 15 May 2009, leg. B.R. Kropp, BK15-May-2009-10a (UTC255959).

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